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Estimating bird species richness: How should repeat surveys be organized in time?

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Abstract Estimates of species richness for a given area require that repeat surveys be taken, so that the statistical robustness of the estimate can be assessed. But how should these repeat surveys be organized in time? Here we present a case study of Australian woodland birds, surveyed using the 'active timed area search' method, which has become the standard unit for the Australian Bird Atlas, a continental-scale bird survey. To date, there has been no assessment of how estimates of species richness derived from this method are affected by the temporal organization of the repeat surveys. For instance, can conducting the repeat surveys in sequence on the same day effectively capture richness, or will additional species be obtained by repeating the surveys on different days within a season? If so, does the spacing of the repeat visits throughout the season have an effect? To answer these questions, we surveyed woodland birds in the Mount Lofty Ranges, South Australia, during late spring–summer 1999–2000, and compared the performance of two different temporal configurations of repeat visits to sites: (i) six repeat surveys performed on the same day; and (ii) three repeat surveys on different days. For both, we calculated the average number of species actually sighted and also estimated total species richness. The data supported our hypothesis that the same-day surveys would yield fewer species and underestimate total species richness. The different-day repeats captured significantly more species per unit of survey effort, and yielded a higher richness estimate. However, the timespan over which different-day surveys were conducted within a season did not have a significant influence on species richness estimates, evincing a qualitative advantage to surveying on different days, regardless of the spacing of repeat visits. These results may be of assistance to conservation managers when planning cost-efficient monitoring regimes.

Key words: monitoring, Mount Lofty Ranges, species accumulation curves, survey method, woodland birds.

INTRODUCTION

There are almost as many techniques for sampling species distribution and abundance as there are kinds of taxa to sample. Within Australia alone, a wide range of techniques is used for conducting avifaunal surveys (Recher 1988). One such technique is the 'active timed area search method' for censusing forest birds (Loyn 1986). This method, in which an observer records numbers of each species seen while actively searching a certain area over a fixed time period (usually 2 ha and 20 min), is the basis for the ongoing continental-scale avifaunal survey of Australia, the Birds Australia Atlas project. Field testing revealed that this method was the most effective of four trialled, in terms of detecting individuals and species, minimizing bias due to time of day and weather, and retaining popularity with observers (Hewish & Loyn 1989).

Given that many professional ornithologists and biological survey teams may now adopt the 20 min-2 ha method in order to make their data compatible with that in the Atlas, the method is likely to play an increasingly prominent role as a tool for making conservation management decisions for birds in Australia. We therefore thought it timely to conduct some further investigation into its performance. We pose a series of questions regarding this survey method, aimed at deducing how its results vary over different temporal scales. For example, in order to estimate species richness using species accumulation curves, it is necessary to take multiple samples from a given site (Soberón & Llorente 1993; Colwell & Coddington 1994). But is it sufficient to visit the site once and perform multiple repeated counts on the same day, or will more species be observed by distributing the same survey effort across different days? If so, does the temporal spacing of surveys influence the number of species recorded? Is one approach more efficient than the other in terms of species recorded per unit time, and is the final predicted level of species richness statistically different between the two approaches?

Another motivation for our study was the fact that if patches are not in very close proximity, for example when conducting regional surveys, it is tempting to take the approach of visiting each site once only, but

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spending a large block of time (e.g. multiple same-day 20-min counts) there, in the hope of reaching a point of diminishing returns on the species accumulation curve. This approach promises an increase in time-efficiency over carrying out single 20-min counts at each site on different days and incurring a travel-time cost for each count. However, we hypothesized that repeated same-day counts on a single day might fail to register the presence of species that move in and out of a survey site from day to day. Such species could conceivably be resident in an area including a survey site, but might not visit every portion of it, for example the chosen survey site itself, within a given 2-h period. Therefore the same-day counts would be more likely to miss recording these species, leading to an under-estimate of species richness. If such an approach were to be used for management purposes, where it is critical to detect the presence or absence of individual species, and changes in overall avifaunal species richness, this is important information.

In the present paper we address the questions outlined previously by comparing the performance of 'same-day' as opposed to 'different-day' 2 ha-20 min surveys using species accumulation curves and estimates of overall species richness. Using terrestrial birds in stringybark woodlands in the Mount Lofty Ranges of South Australia, we compare six 'same-day' visits with three 'different-day' repeat visits. For each approach, we calculate the trajectory of the species accumulation curve and its predicted final asymptote (i.e. the total species richness), using maximum likelihood methods (Raaijmakers 1987). We also examine the dependence of species richness estimates in the different-day surveys on the temporal spacing of repeat visits. The results are of potential importance not only for ornithologists planning survey and monitoring programmes based on the active timed area search method, but for practitioners of biological surveys in general.

METHODS

Data collection

The study was conducted in remnant patches of stringybark woodland in the high rainfall areas of the southern Mount Lofty Ranges, South Australia. The patches were of relatively uniform habitat type, in which the tree cover was wholly or mostly (>90%) messmate stringybark, *Eucalyptus obliqua* (36 patches), or brown stringybark, *Eucalyptus baxteri* (two patches). This is the most abundant and widespread class of native vegetation remaining in the southern Mount Lofty Ranges, enabling us to obtain data from a wide range of patch sizes (4–1686 ha) evenly spread over a broad geographical area (approximately 150 km × 40 km, from Morialta Conservation Park in the north (138°43.44′E, 34°54.22′S) to Deep Creek Conservation Park in the south (138°13.70′E, 35°36.01′S). Thirty-eight sites within this area were selected (Fig. 1). Surveys were undertaken over spring–summer between 8 November 1999 and 24 February 2000, starting no earlier than 05.45 hours and finishing no later than 14.00 hours (Australian Central Standard Daylight Saving Time). Migrant species to the region such as kingfishers and cuckoos typically arrive well before this starting date and remain until the autumn, justifying our assumption that the bird community was relatively unchanging for the duration of the study.

We used the 20 min-2 ha search method (Loyn 1986). Sites were circumscribed by pacing out a 2-ha area and only those birds using the habitat within this area were recorded. This included birds seen perching within the site, or heard calling from a stationary position within the site for part or all of the 20-min survey period. Birds flying over or through the site but not alighting were not included, with the exception of swallows, martins, woodswallows and birds of prey that were actively foraging.

Two series of visits were made to each site, a same-day series and a different-day series. In the same-day series, one observer visited the site on one day and performed six sequential 20-min surveys of the 2-ha area, for a total of 2 h. In the different-day series, different observers visited the site on three separate days (6–93 days apart) and performed a single 20-min count on each day. Surveys were carried out by five experienced observers and to reduce the effects of

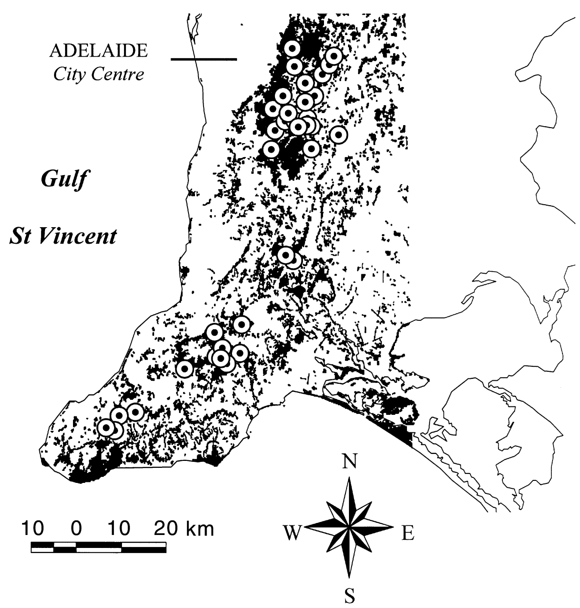

Fig. 1. Map of the study region, showing (■) remnant vegetation and (⦿) the location of survey sites.

observer variability (Cunningham *et al.* 1999), visits to each site were allocated as evenly as practicable among observers.

Species richness in same-day versus different-day surveys

To test the hypothesis that fewer species would be recorded on a single day compared with multiple days, we calculated species accumulation curves for both the same-day and different-day techniques. When calculating mean cumulative species numbers after each visit for each survey type, bias due to the ordering of repeat visits was countered by using six permutations of the actual order. In the different-day surveys, each site received three visits, yielding a total of 3! = 6 possible permutations (1-2-3, 1-3-2, 2-1-3, etc.). Thus at each site, there were six possible trajectories for the species accumulation curve. For each site and visit, we took the mean of these six numbers, leaving us with 38 mean species numbers for each of the three visits within a site. We then calculated the mean (±95% confidence interval) of these 38 means to represent the overall mean across sites at each visit for this survey technique. To calculate confidence intervals, the central limit theorem was invoked to justify the normal approximation, on the grounds that the cumulative number of species observed at a site was a random variable derived from the sum of multiple binomial distributions (presence/absence and observation/non-observation of each of approximately 107 species likely to be found in the Mount Lofty Ranges (see Ford & Howe 1980)). For the same-day surveys, there were 6! = 720 possible permutations. To maintain consistency with the different-day method, only six of these were selected at random in order to calculate means.

The asymptotes of the species accumulation curves were calculated by fitting a two-parameter hyperbolic function to the data (Colwell & Coddington 1994):

$$S(n) = S_{\max} - \frac{\beta S(n)}{n} \tag{1}$$

where $S(n)$ is the cumulative number of species obtained after n visits, $S_{\max}$ is the total number of species in the site, and β is a fitted constant. This is known as the Eadie–Hofstee equation and is recommended by Colwell and Coddington (1994) as being least likely to produce biased estimates. If $Xi = S(n)/n$ and $Yi = S(n)$, then Raaijmakers (1987) showed that the maximum likelihood estimate for β is

$$\hat{\beta} = \frac{\bar{X}S_{yy} - \bar{Y}S_{xy}}{\bar{Y}S_{xx} - \bar{X}S_{xy}} \tag{2}$$

where S_{xx}, S_{yy} and S_{xy} are the sums of squares and cross-products of the deviations $Yi - Y$ and $Xi - X$.

The maximum likelihood estimate for $S_{\max}$ is then

$$\hat{S}_{\max} = \bar{Y} + \beta\bar{X} \tag{3}$$

The variance estimate for β is

$$\text{var}(\hat{\beta}) \approx \frac{\sigma^2}{[(1 + 2\sigma^2 / S_{\max}{}^2)\ \Sigma_{i=1}^{n}\ (U_i - \bar{U})^2]} \tag{4}$$

with

$$\sigma^2 = \frac{S_{yy} + 2\hat{\beta}S_{xy} + \beta^2 S_{xx}}{n - 2} \tag{5}$$

$$U_i = \frac{\mathrm{S}_{\max}}{\mathrm{s}_i + \beta} \tag{6}$$

where s_i is the ith repeat visit to a particular site and

$$\text{var}(\hat{S}_{\max}) \approx \frac{\sigma^2}{n} + \bar{U}^2\ \text{var}(\hat{\beta}) \tag{7}$$

In addition to species accumulation curves, we also calculated the probability of having obtained more species after a certain number of different-day visits than after an equal number of same-day visits. This is

$$\mathrm{P}_n(x) = \sum_{y=0}^{\infty} \mathrm{a}_n(y)\, b_n(y - x)\, dy \tag{8}$$

where $P_n(x)$ is the probability of obtaining x more species after n visits in a different-day versus same-day survey, $a_n(x)$ is the probability of obtaining x species by visit n of a different-day survey (n = 1, 2, 3), and $b_n(x)$ is the probability of obtaining x species by visit n of a same-day survey.

The quantities $a_n(x)$ and $b_n(x)$ were derived empirically by calculating, for each visit and both survey types, the proportion of patches in which x species had been seen by visit n. For example, after three different-day surveys, there were eight patches in which 17 species had been discovered, so $a_3(17) = 8/38 = 0.21$. As numbers of species found in the different-day ($a_n(x)$) and same day ($b_n(x)$) surveys were found to be Poisson-distributed for each n (Kolmogorov–Smirnov test, $K_s < 0.14$, $P > 0.31$ in all cases), the predicted values of $P_n(x)$ were

$$\mathrm{P}_n(x) = \sum_{i=1}^{\infty} \frac{\lambda_{d(n)}^{i} \exp^{-\lambda d(n)}}{i!} \cdot \frac{\lambda_{s(n)}^{i-x} \exp^{-\lambda s(n)}}{(i-x)!} \tag{9}$$

where $\lambda_{d(n)}$ mean cumulative number of species obtained by the nth visit of the different-day surveys, $\lambda_{s(n)}$ is the mean cumulative number of species obtained by the n^{th} visit of the same-day surveys.

In practice, $P_n(x)$ was summed only over i = 1–35, as this was found to capture at least 99.9% of the probability for each n. Confidence intervals for each $P_n(x)$ were calculated by resampling a Poisson distribution with the same mean and variance as those estimated from the data, and taking the upper and lower 2.5% points.

Observer effects

In some woodland bird surveys, it has been shown that the probability of observing certain species varies among different observers (Cunningham *et al.* 1999). Therefore, if different observers visit a site, more species (or fewer species, depending on which of the observers is more biased) may be recorded compared with those that would have been recorded by a single observer. To ensure any apparent difference between same-day and different-day surveys (that is, higher counts in the different-day surveys; Fig. 2) was not an artefact of this observer effect, we checked whether the number of different observers visiting a site in the different-day surveys influenced the total number of species recorded there over the three visits. To do this, we used a generalized linear model, with number of species recorded as the response variable (Poisson-distributed) and number of observers as the explanatory variable.

To calculate the statistical power of this test, we simulated data collected by either two or three observers from Poisson distributions. We fixed the overall mean to be the same as our original data (17.1 spp.) for all effect sizes. The actual mean was either decreased or increased from this global mean by the same amount for both categories. The value of power quoted in the results is for the effect size observed in our surveys, a mean difference of 2.81 species between same-day and different-day surveys after three repeat visits (Fig. 2).

Effect of temporal spacing of repeat visits in different-day surveys

To test the hypothesis that the timespan over which repeat visits were made in the different-day surveys had a positive effect on the number of species recorded, we employed a Bayesian regression analysis. In this approach, a prior distribution for the parameter of interest (in this case the slope of a regression of number of species on timespan between first and last visits to a site) was combined with a likelihood function fitted to the data, to yield a posterior estimate of the parameter's distribution (for a similar example, see Wade (2000)). In the absence of previous data to suggest the form of the slope's distribution, we used a uniform prior distribution, and fitted a normal likelihood to the data. As mentioned previously, the choice of a normal likelihood is justified by the fact that the cumulative number of species recorded at each site is the sum of many binomial distributions and therefore, by the Central Limit Theorem, approximately normal. With a uniform prior and normal likelihood, the resultant posterior distribution is a *t*-distribution with degrees of freedom equal to the sample size minus two (Bernardo & Smith 1994). The mean and 95% confidence intervals for the slope were taken from this distribution.

The Kolmogorov–Smirnov test and the Poisson GLM with power analysis were run in SPLUS 4.0: the models using inbuilt statistical options and the power analysis by running a simulation coded in SPLUS script. All other analyses were carried out using Visual Basic macros to manipulate data within Microsoft Excel 7.0a spreadsheets.

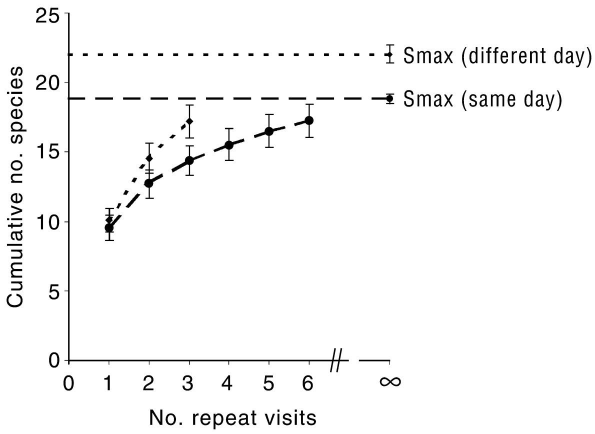

Fig. 2. Species accumulation curves and total species richness (S_{max}) estimates obtained using two survey methods: (- - -) three repeat counts performed on different days and (— — —) six repeat counts performed on the same day. Error bars are 95% confidence intervals.

RESULTS

Species richness in same-day versus different-day surveys

The different-day surveys yielded consistently higher species counts than the same-day surveys, for the same survey effort (Fig. 2), consistent with our first hypothesis. The Poisson GLM yielded no detectable effect of the number of observers visiting a site on the

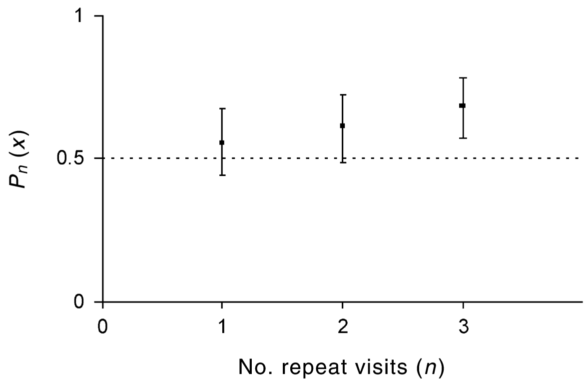

Fig. 3. Probability (±95% confidence intervals) of obtaining more species for a given surveying effort from the different-day visits as opposed to same-day visits ($P_n(x)$).

cumulative number of species recorded at that site ($\chi^2 = 0.97$, d.f. = 1, $P = 0.44$, power = 0.48), suggesting that the difference between the two methods was not due to interobserver variability. As expected, the mean number of species obtained from the initial visit of each survey method was not statistically distinguishable (at $\alpha = 0.05$). However, by the third visit, the mean cumulative number of species obtained from the different-day method was significantly greater than that from the same-day method (Fig. 2). Furthermore, the mean from the sixth same-day visit was not significantly greater than that from the third different-day visit (Fig. 2). In other words, the different-day method detected approximately as many species (17.18 ± 1.21, mean ± 95% confidence interval) as the same-day method (17.26 ± 1.20), but with half the surveying effort. In line with these results, the probability of obtaining more species for a given surveying effort from the different-day visits as opposed to the same-day visits showed a trend toward increasing with each repeat visit, and was significantly greater than 0.5 by the third visit (Fig. 3).

The steeper accumulation of species in the different-day method suggested that it would also yield a higher asymptote: S_{max} was estimated at 22.04 ± 0.63 for the different-day method and only 18.83 ± 0.32 for the same-day method (Fig. 2). Note also that the upper confidence limit for the final same-day survey (18.46) is similar to the lower confidence limit of the asymptote for this method (18.51), suggesting that an increase in survey effort for this technique is unlikely to result in new species being detected. In contrast, there is a substantial gap between the upper confidence limit for the final different-day survey (18.39) and the lower confidence limit of the asymptote (21.41), indicating that the species accumulation curve for this method has not begun to level out after three visits, and further surveying effort will be rewarded by the addition of more species to the list.

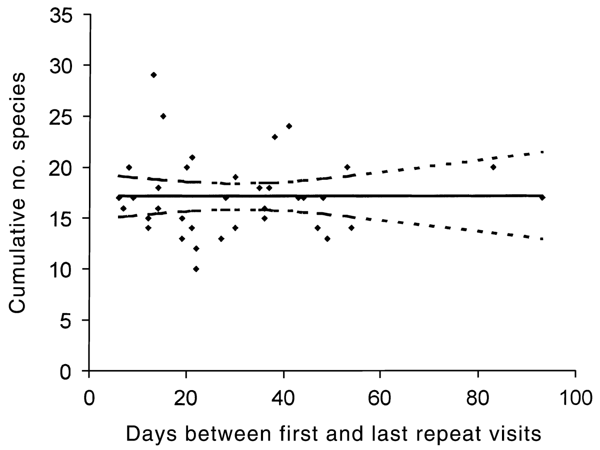

Fig. 4. Cumulative number of species recorded at a site as a function of the number of days between first and last visits. (——) Fitted regression line; (- - -) 95% confidence intervals; $y = 0.0007x + 17.16$; $R^2 = 0.000002$.

Effect of temporal spacing of repeat visits in different-day surveys

The regression analysis yielded evidence that the temporal spacing of repeat visits on different days had little impact on the number of species recorded (Fig. 4). Although the estimate of the slope (±95% confidence interval) was positive (0.00075 ± 0.07), its magnitude was extremely small and the confidence interval (0.07075, –0.06925) was essentially centred around zero. Removal of two outlying observations (outlying with respect to the independent variable: $x = 83$ and 93) slightly affected the sign and magnitude of the slope estimate (–0.018 ± 0.09), but not the biological conclusion.

DISCUSSION

As predicted, repeating 2 ha-20 min counts on different days results in higher numbers of species being observed than an equivalent amount of survey effort concentrated on a single day. In terms of actual surveying time, this makes the different-day method significantly more efficient than the same-day method. However, in our study this advantage was more or less neutralized by the greater travel time incurred by spending only 20 min at each site in the different-day method. Overall, travel times between patches averaged approximately 30 min, giving an average total time to implement each different-day 20-min count of 50 min, whereas six same-day counts could be performed in 2 h 30 min, at an average of 25 min per count. Thus a typical morning of surveying (approximately 5 h) could only yield six different-day 20-min counts, but 12 same-day counts. Thus although there was no statistical difference between cumulative species numbers after three different-day counts and six same-day counts (Fig. 2), this does not necessarily imply that the different-day counts were twice as economical. Once travel time is taken into account, the two methods were of approximately equal cost per species recorded. Survey sites would need to be substantially more clumped than in our study in order for the different-day method to overcome the travel time deficit. If sites were much more widely dispersed, the same-day method would be more efficient.

However, there was an important sense in which different-day counts were clearly superior to same-day counts. The predicted asymptote of the species accumulation curve (i.e. the estimated total species richness) was significantly higher for different-day counts than for same-day counts. Our interpretation of this result is that some of the birds that were resident in the patch had home ranges larger than 2 ha, and moved around them over time periods greater than a day. If such a bird happened to leave the 2-ha area just before a same-day count began, it would not be recorded. However, if this occurred in a different-day count, there would still be two further opportunities for it to arrive in the site during a survey. We note that detailed quantitative information on species' home ranges and rates of movement would be required to demonstrate that this mechanism accounts for our results. However, the point remains that same-day counts appear to underestimate species richness significantly, an important fact for conservation managers to consider when planning avifaunal surveys.

Our result that the temporal spacing of repeat visits within a season does not influence the number of species recorded may also be useful in a survey planning context. Although it is important to revisit the same site on different days, it appears not to matter whether those repeat visits are close together or far apart in time. Provided that the visits are conducted within a survey period during which the species composition of the assemblage being surveyed is roughly constant, our results suggest that they will yield the maximum number of species possible. The time intervals between our different-day surveys ranged up to 93 days, but represent just a single season of the year. Had we spread our repeat samples out over the entire year (or across different years), the richness estimate would almost certainly have been higher, because of seasonal turnover in the species composition of the assemblage. This could be a worthwhile topic for future studies to address.

In summary, we have shown that there is a qualitative difference between species richness estimates obtained from repeat surveys on a single day, and those obtained by repeat surveys on multiple days. Although we employed just one method out of the many survey techniques available for birds, we expect that this result may hold for other bird survey methods, and perhaps any kind of survey that targets mobile organisms in which species composition at a site may vary from day to day. A clear recommendation for the practitioners of biological surveys is that repeating surveys on different days is essential in order to capture the species richness that exists at a site.

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